9 The place of basidiomycetes in the decay of wood in contact with the ground

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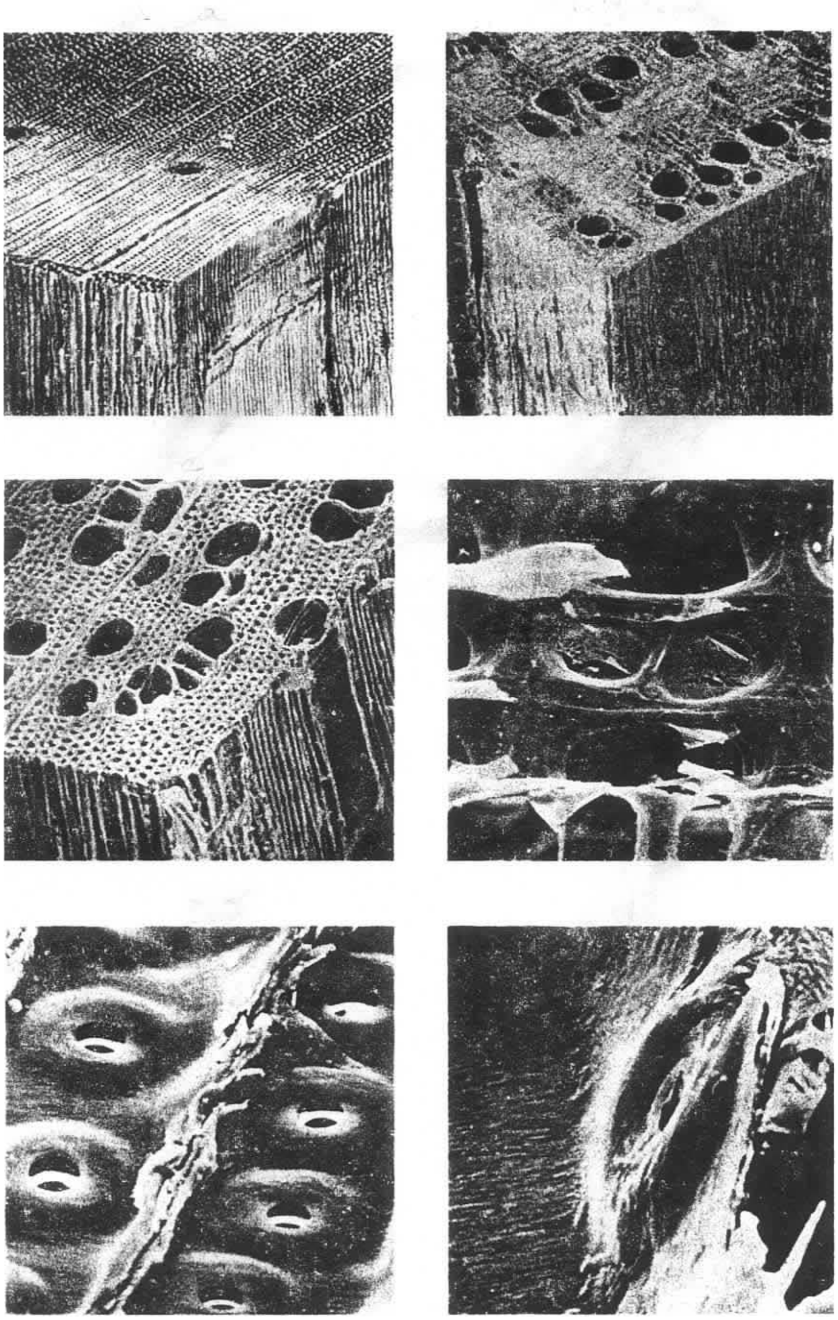
Wood: food source, substrate and environment

To the wood-rotting micro-organisms colonising it, wood consists of a series of conveniently orientated holes surrounded by food. The shape, size and orientation of the holes relate directly to the anatomy of the species of wood being colonised, and differences in the chemical constitution of the cell walls or cell contents may affect the ability of a particular fungus to utilise them as a nutrient source.

Softwoods (gymnosperms) are formed largely by tracheids, with the cell lumen completely enclosed by a cell wall, so that movement of water or micro-organisms must involve passage through a cell wall or pit membrane (Fig. 1*a*). Hardwoods (angiosperms), however, consist of vessels, fibres and parenchyma as well as some tracheids, and here the vessels are often formed from open-ended vessel elements so that both water and micro-organisms can move along the grain without necessarily passing through either a cell wall or pit membrane (Fig. 1*b,c*). In addition, the hemicellulose component of the cell wall differs between softwood and hardwood, and in both groups there is a considerable difference between sapwood and heartwood of the same species. Sapwood is likely to contain accumulated nutrients such as starch, residual protoplasts or lipids stored by the tree in the ray parenchyma which is absent in heartwood. The heartwood is likely to have additional materials deposited in the cell walls during the process of heartwood formation. Such materials are known as *extractives* and often provide the dark colouration typical of such woods as mahogany (*Swietenia macrophylla*), teak (*Tectona grandis*), or ebony (*Diospyros* spp.). In some heartwoods these extractives have some degree of toxicity to micro-organisms and may impart a natural durability, as is shown in western red cedar (*Thuja plicata*), teak, or greenheart (*Ocotea rodiaei*).


a
c

The colonisation sequence of wood by micro-organisms and the development of decay will be affected by these differences as shown in the case of commercial timbers by Dickinson (Chapter 10). Structural and chemical differences constitute part of the ecological factors that will determine the process of decay. Other factors include: the rate of growth of the wood when it was being formed in the tree; the orientation of the grain of the wood with respect to the source of invading organisms and water; the moisture content of the wood, both static and in movement; the presence, movement or accumulation of nutrients; pH and temperature. Such factors give rise to a series of ecological niches which may be filled by a range of micro-organisms depending upon the particular circumstances.

Micro-organisms associated with decay of wood in contact with the ground

A wide range of micro-organisms from many diverse taxonomic groups are readily available to colonise and destroy wood in contact with the ground. Some are specific to a particular wood under certain precise conditions of exposure. Others are more opportunist and may play a different rôle in the decay process under varying conditions. It is not possible to define or restrict each decay type within taxonomic frontiers, since the same organism (e.g. *Phialophora fastigiata*) may, given suitable environmental conditions, fill one or several ecological niches or 'physiological groups' (Clubbe, 1978).

Studies on the micro-organisms colonising wood and on the sequence of events leading to the onset of decay have shown the importance of reclassifying the species involved, irrespective of their taxonomic identity, into a small number of groups relevant to their effect on the wood (Banerjee, 1969; Banerjee & Levy, 1971; Butcher, 1968*a,b*, 1971; Carey, 1980; Clubbe, 1978, 1980; Corbett, 1963; Corbett & Levy, 1963; Cowling, 1965; Greaves, 1966; Käärik, 1967, 1968; Levy, 1968, 1971, 1973, 1975; Merrill & French, 1966). Clubbe (1980) recognised six such

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Fig. 1.(*a*) Softwood anatomy: Scots pine (*Pinus sylvestris*), × 35. (*b*) Ring-porous hardwood anatomy: oak (*Quercus robur*), × 30. (*c*) Diffuse-porous hardwood anatomy: birch (*Betula pendula*), × 120. (*d*) Breakdown of the membrane of crossfield pits in Scots pine by bacterial action, × 600. (Zainal, 1976*b*.) (*e*) Bordered pits in Scots pine, showing complete breakdown of the pit membrane by bacterial action, × 500. (*f*) Bacteria associated with breakdown of the membrane of an aspirated bordered pit in Scots pine, × 700.

groupings, based on his own observations and other studies published in the literature. They comprised:

Bacteria
'Primary moulds'
'Stainers'
'Soft rots'
Basidiomycetes { White rots / Brown rots
'Secondary moulds'

which may be defined as follows.

Bacteria

This group includes a range of true bacteria, mainly gram-positive rods, some of which are capable of fixing atmospheric nitrogen. It also includes some actinomycetes such as *Streptomyces* species, which often show a somewhat random distribution. These micro-organisms are usually the first colonisers and may have one or several effects on the wood. (*a*) A progressive breakdown of the membrane of pits in the sapwood is evident (Fig. 1*d–f*). This opens up the wood structure, allows gaseous diffusion to occur, provides an open pathway for water, and gives access to colonising micro-organisms incapable of causing lysis of a wall or pit (Levy, 1973, 1975). (*b*) Fixation of atmospheric nitrogen has been demonstrated to increase progressively from an exposed surface into wood (Levy, Millbank, Dwyer & Baines, 1974; Baines & Millbank, 1976; Baines, Dickinson, Levy & Millbank, 1977). This could provide an additional source of nitrogen, increasing the low level normally found in wood. (*c*) There is antagonism or synergism with fungal colonists (Levy, 1975). (*d*) The presence of bacterial cells and their metabolic products will have changed the internal environment, although no other effect may be observed.

'Primary moulds'

These organisms comprise the first fungal colonists, and can be regarded as akin to Garrett's sugar fungi (Garrett, 1951, 1955). They do not appear to possess enzymes capable of degrading cellulose or lignin and do not seem able to attack the wood cell walls. Their food source is likely to be sugars or simple carbohydrates either present in the ray parenchyma of the sapwood or derived from the soil. They can penetrate into wood only through natural openings, such as end-grain apertures or openings through the walls produced by other organisms, i.e. through pits after bacteria have destroyed the pit membrane. Phycomycetes, ascomycetes, and fungi imperfecti are all represented in this group.

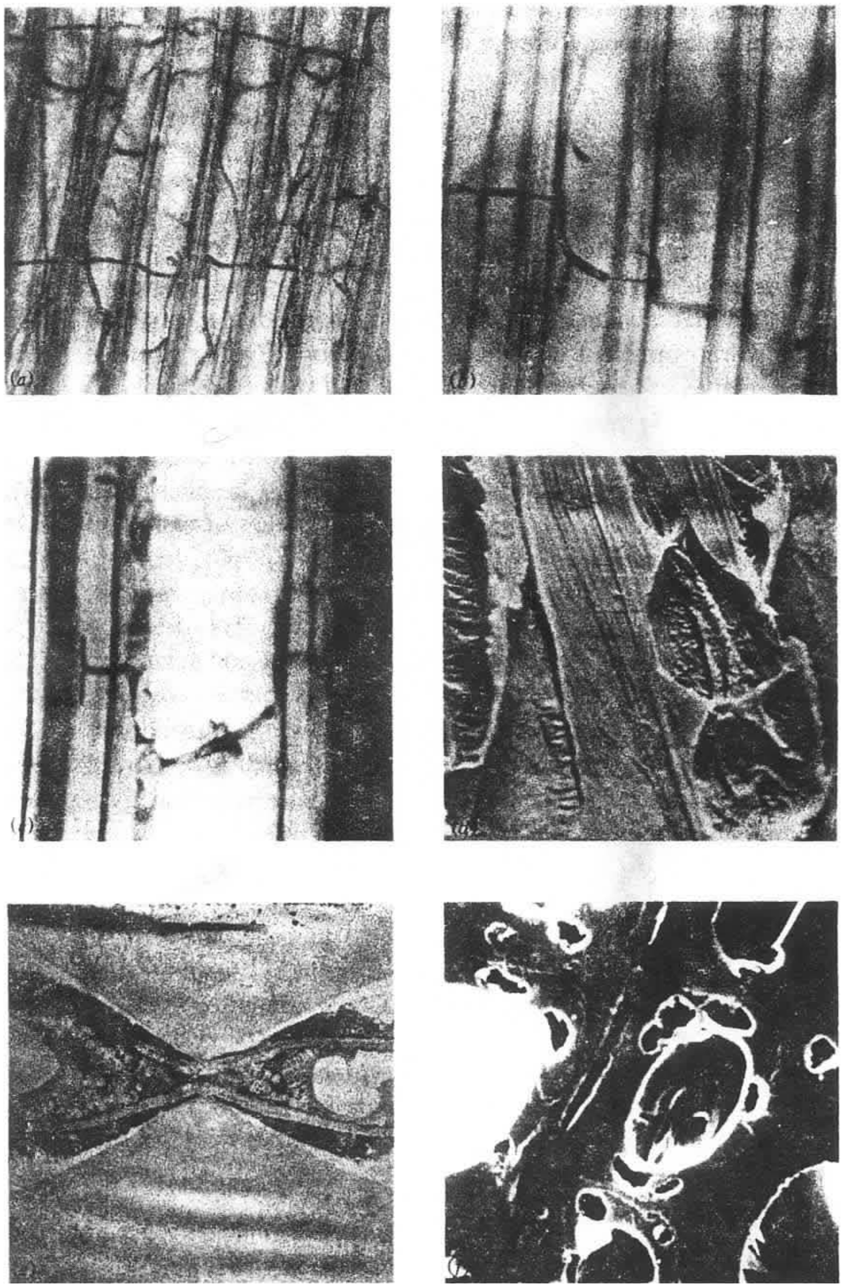
'Stainers'

This group, mainly ascomycetes and fungi imperfecti, is characterised by the pigmentation of the hyphal walls, which gives rise to a discolouration of the sapwood of infected wood. Like the 'primary moulds' their nutrients are primarily the food reserves of the tree stored in the ray parenchyma of the sapwood, or residual sugars and simple carbohydrates present elsewhere in the wood. Hyphae of these organisms are able to penetrate through cell walls in a characteristic manner by means of a fine constriction of the hypha in the wall and resumption of its normal size and shape on emergence into the lumen (Fig. 2*a*); a single hypha may pass through a number of cells in this way (Fig. 2*b*). Several 'stainers' have been shown to be capable of causing soft rot in wood.

'Soft rots'

This group is comprised of ascomycetes and fungi imperfecti. They are the first of the wood-rotting fungi to colonise wood in ground contact. They are grouped together on the basis of forming cavities in the S_2 layer of the cell wall (Käärik, 1974), which is destroyed by the formation of chains of such cavities. Their micromorphology was first illustrated in the middle of the last century, but their economic significance was not realised until nearly a hundred years later. Findlay & Savory first reported their activities in 1950, and Savory (1954*a,b*, 1955) published a series of papers which established the term 'soft rot'. He demonstrated that the fungi were responsible for the decay of the timber fill in water cooling towers. This degradation was previously thought to be due to chemical breakdown and not to be the result of biological action. The soft-rot fungi become established where there is little competition from other fungi and are known to give rise to serious economic losses of timber. Where the basidiomycetes are able to establish dominance, the soft-rot fungi, although present, never become the main causal organisms of wood decay.

Savory showed that soft-rot fungi grew in the S_2 layer of the secondary cell wall of wood cells, forming chains of cavities with pointed ends which were orientated parallel to the cellulose microfibrils in the cell walls (Fig. 2*c*). However, Corbett (1963, 1965) was the first to observe


(a)
(b)
(c)
(d)
(e)
(f)

the way in which the fungal hyphae penetrated the S_2 layer of the wood cell wall. The details are given so that they can be contrasted with the behaviour of basidiomycetes. A short side-branch of a hypha lying in the cell lumen penetrated the S_3 layer perpendicular to the cell wall, and, on reaching the S_2 layer of that wall (or after having passed into the S_2 layer of the adjacent cell wall), the penetration hypha appeared to turn through an angle of 90° to lie parallel with the cellulose microfibrils, and branched at 180° to form what Corbett called a 'T-branch' (Fig. 2*c*). A cavity was eroded around the hyphal branches forming the cross of the T, and the hyphae increased in girth. Fine hyphal strands, termed 'proboscis' hyphae, (Corbett, 1963, 1965; Crossley & Levy, 1977) formed the initial extension growth of the hypha in the cavity.

Leightley (1977), Leightley & Eaton (1977), and M. Hale (personal communication) studied the development of the proboscis hypha by time-lapse photography. A fine hypha penetrates from the distal ends of the cavities in a direction parallel to the cellulose microfibrils. After a period of growth, further extension of the proboscis hypha ceases; the hypha increases in girth and a new cavity forms around it. After some time, extension growth continues by the development of a new proboscis hypha and the process is repeated time and again (Fig. 2*d*). A hypha in a cavity appears to be capable of forming a new T-branch, so setting up a new helical chain of cavities. The cavity itself is straight-edged even when viewed under a transmission electron microscope (Findlay, 1970) (Fig. 2*e,f*). This suggests that the action of the enzyme in forming the cavity is very exact, and that at no time does the enzyme system diffuse freely into the wood cell wall beyond the sharp edge of the cavity. Montgomery (Chapter 3) and Green (1980) suggest a possible reason for this behaviour.

The pointed ends of the cavities have given rise to much speculation and many authors have attempted to explain their formation in relation

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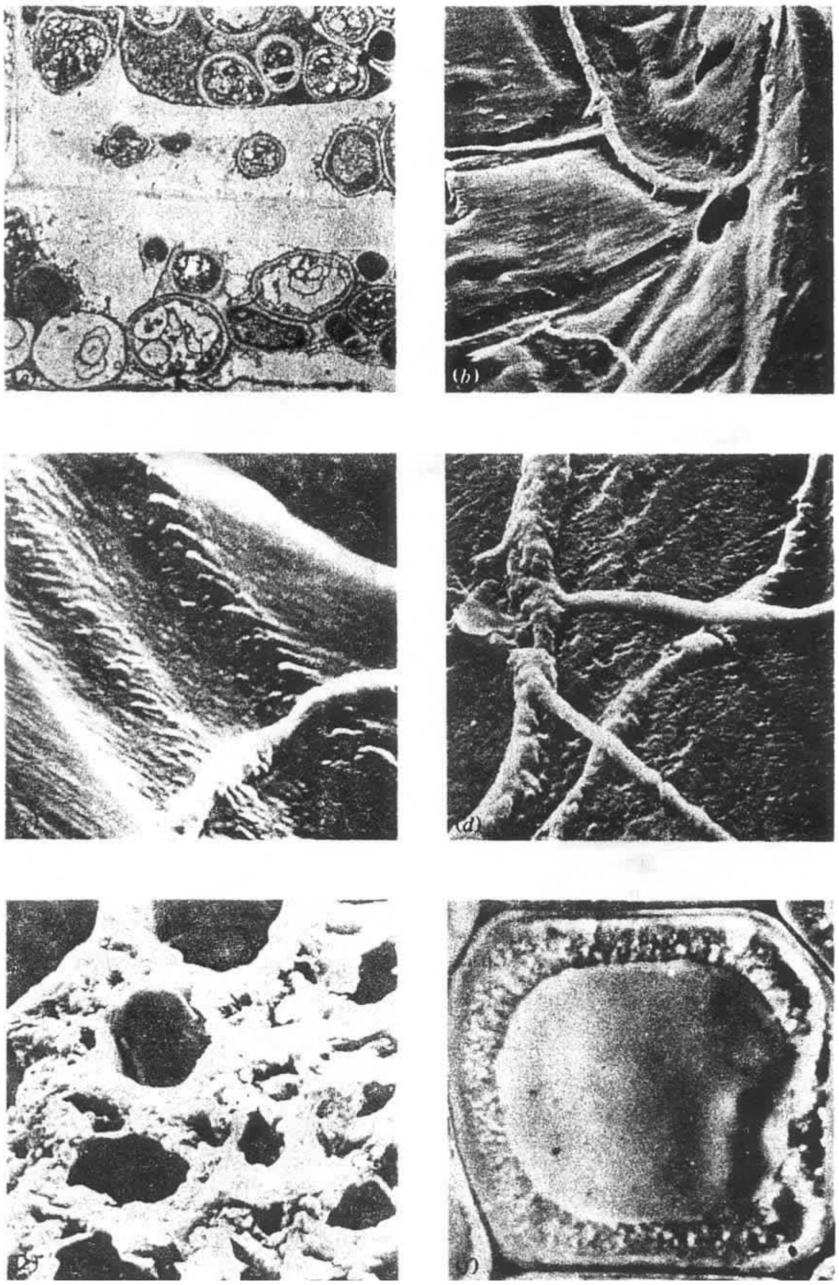
Fig. 2. (*a*) Hyphae of a 'stainer' fungus in birch (*Betula pendula*), showing constrictions in fibre cell walls, × 150. (*b*) Hyphae of a 'stainer' fungus in birch, showing details of the fine constriction within the cell walls of fibres, × 300. (*c*) T-branch of the soft-rot fungus *Chaetomium globosum* in the S_2 layer of the wall of a tracheid of Scots pine (*Pinus sylvestris*), × 600. (G. Stevens.) (*d*) Chain of cavities caused by a hypha of the soft-rot fungus *Phialophora fastigiata* in birch. × 2500. (Findlay, 1970.) (*e*) Pointed ends of two soft-rot cavities showing the sharpness and straightness of the edge of the cavity and the hypha, × 12 000. (Findlay, 1970.) (*f*) Soft-rot cavities seen in transverse section in birch fibres, × 500. (A. Crossley.)


(b)
(d)

to the fine structure of the cell wall. Preston (1979) suggested a mechanism based on the differential rates of flow of the enzyme through the non-crystalline regions of the cellulose microfibrils.

Whatever the mechanism by which these cavities are formed, the effect on the wood structure can be devastating. Zainal's transmission electron photomicrographs (Zainal, 1976*a,b*) (Fig. 3*a*), show that the entire secondary wall apart from a residue of the S_3 layer can be removed during soft-rot attack on a birch (*Betula*) fibre. Dickinson (Chapter 10) points out the importance of the decay by these organisms when basidiomycetes do not develop.

Basidiomycetes

Until 1950, when Findlay & Savory first reported soft-rot fungi, basidiomycetes were regarded as the only fungi capable of causing severe economic loss of timber. White rots destroy both the holocellulose and lignin in the wood cell walls, bleaching the wood, whereas the brown rots utilise the holocellulose, leaving the lignin of the wood as a brown, brittle, and friable residue (see Hering: Chapter 12; Hintikka: Chapter 13).

Bravery (1971, 1972, 1975 and 1976) published an outstanding series of scanning electron photomicrographs, which illustrated another fundamental difference between the attack by white-rot and brown-rot fungi. His observations were confirmed by Nasroun (1971) with other basidiomycetes. Bravery showed that the hypha of a white-rot fungus penetrated into the cell lumen and lay on the inner surface of the wood cell wall. Lysis of the wall occurred along the hyphal contact, forming a groove or trough with a central ridge on which the hypha rested. As the

Fig. 3. (*a*) Cell wall of birch fibre almost completely destroyed by the soft-rot fungus *Phialophora fastigiata*, apart from the middle lamella complex and the S_3 layer, × 7000. (Zainal, 1976*b*.) (*b*) Troughs formed in the cell wall by hyphae of the white-rot fungus *Coriolus versicolor* in Scots pine (*Pinus sylvestris*), × 1000. (Bravery 1972.) (*c*) Part of Fig. 3(*b*) at a higher magnification to show the ends of the cellulose microfibrils visible at one side of the trough. × 3000. (Bravery, 1972.) (*d*) Hyphae of the brown-rot fungus, *Coniophora puteana*, showing that troughs are absent from region round the hyphae, × 3000. (Bravery, 1972.) (*e*) Transverse section of brown-rotted wood to show the destruction of part of the cell wall whilst the S_3 layer remains intact, × 250. (Nasroun, 1971.) (*f*) Transmission electron micrograph of a birch (*Betula pendula*) fibre decayed by the brown-rot fungus *Coniophora puteana*. Note the hypha in the cell lumen. (A. Crossley.)

hypha branched, so new troughs were formed and eventually the troughs coalesced, eroding the wall of the wood cell (Fig. 3*b*,*c*). The hypha was able to penetrate through the S_3 layer of the cell wall and well into the S_2; if the trough was parallel to the microfibrils its edges were smooth, but if it cut across their orientation the edges were ragged and the ends of the cellulose microfibrils could be seen clearly (Fig. 3*c*). The formation by white-rot fungi of troughs in the cell wall suggests some restriction to the free diffusion of enzyme away from the hypha. Montgomery (Chapter 3), Green (1980) and Green, Dickinson & Levy (1980) give possible explanations for these characteristics.

The brown-rot fungi show a different micromorphology (Bravery 1971; Nasroun, 1971). The hypha again penetrates the lumen and lies on the inner surface of the cell wall. The appearance of both the hypha and the S_3 wall layer change very little, but the other layers are completely altered by breakdown of the holocellulose. The resulting friable residue, with its high lignin content, looks more like expanded polystyrene or foam rubber than the normal smooth texture of unattacked walls (Fig. 3*d*–*f*). In this case, enzyme movement appears to be unrestricted and the enzyme system seems to diffuse completely through the wall layers, although it does not penetrate through the primary wall–middle lamella complex into adjacent cells (A. Crossley, unpublished) (Fig. 3*e*,*f*). Montgomery (Chapter 3) and Green (1980) discuss the characteristics of the polysaccharase enzyme system in brown-rot basidiomycetes.

'Secondary moulds'

The final group of organisms are the 'secondary moulds'. This grouping includes all those fungi which do not appear to attack wood itself but possess an active cellulase system, as exemplified by a clearance of ball-milled cellulose in agar culture. Their position in the succession seems to be associated with the appearance and eventual dominance of the decay fungi, particularly the basidiomycetes. The rôle of these 'secondary moulds', predominantly *Trichoderma viride* and *Gliocladium roseum*, is probably one of utilising the cellulose, derived from the breakdown of the wood, which is in excess of the requirements of the decay fungi. This cellulose food source may be a true nutritional excess, or the result of competition between the two groups of organisms for the partially decayed substrate.

Table 1 shows an example of the grouping of organisms isolated from posts in a field experiment.

Table 1. *Species isolated from stakes of* Betula *and* Pinus sylvestris *which had been in the ground for one year.* (After Clubbe, 1980.)

BACTERIA
Various unidentified cultural forms – mainly gram-positive rods
Actinomycetes

'PRIMARY MOULDS'
Arthrinium state of *Apiospora montagnei*
Botrytis cinerea
Cylindrocarpon destructans
Cylindrocarpon state of *Nectria coccinea*
Fusarium sambucinum
Fusarium avenaceum
Fusarium spp.
Mucor hiemalis
Mucor plumbeus
Penicillium cyclopium
Penicillium fennelliae
Penicillium purpurescens
Pestalotia sp.
Trichoderma viride
Verticillium lecanii
Verticillium psalliotae
Yeasts
Zygorhynchus heterogamus
Mycelia sterilia

'STAINERS'
Aphanocladium sp.
Aureobasidium pullulans
Botryodiplodia theobromae
Ceratocystis sp.
Cladosporium herbarum
Coniochaeta subcorticalis
Coniothyrium fuckelii
Drechslera dematioidea
Epicoccum purpurascens
Phialophora fastigiata
Phialophora melinii
Scytalidium sp.
Torula herbarum
Phoma fimeti
Phoma spp.
Xylaria sp.
Mycelia sterilia

'SOFT ROTS'
Coniothyrium fuckelii
Drechslera dematioidea
Epicoccum purpurascens
Humicola fuscoatra
Trichocladium opacum
Phialophora fastigiata
Phialophora melinii
Phialophora spp.
Mycelia sterilia

BASIDIOMYCETES
Sistotrema brinkmannii
Unknown IC/CC/BS7

White Rots
Bjerkandera adusta
Phlebia radiata
Stereum hirsutum
Unknown IC/CC/BS2
Unknown IC/CC/BS4
Unknown IC/CC/BS13
Unknown IC/CC/BS17

'SECONDARY MOULDS'
Acremonium strictum
Gliocladium roseum
Trichoderma viride

Water and nutrients

Corbett (1963, 1965) demonstrated the importance of cellular orientation by showing that fungal hyphae pass quickly through wood along the grain, i.e. from transverse face to transverse face, and more slowly across the grain along the rays, i.e. from tangential face to tangential face. The slowest penetration occurred across both grain and rays, i.e. from radial face to radial face. Here access must involve passage through either cell walls or pits or both. Bravery (1972) pointed out that this was also true for movement of liquids through wood.

A useful example of wood in ground contact is provided by fence posts (Levy, 1968) (Fig. 4). These contain a vertical zonation of microhabitats and yet are basically similar in structure throughout their length. For example, four moisture zones can be found: (*a*) conditions of intermittent wetting and drying; (*b*) permanent low water content; (*c*) permanent high water content, and (*d*) excess water producing anaerobiosis. The variety and activity of the micro-organisms in each zone differ, and this progressively increases the difference between each zone in what is otherwise a relatively uniform structure of void spaces and cell walls. Baines & Levy (1979) demonstrated that a stick of wood with the grain parallel to its long axis will act as a wick if there is a moisture gradient between the two ends. They quantified this wick action by measuring the rate of water movement through sticks of Scots pine (*Pinus sylvestris*) under different rates of evaporation. E. F. Baines (pers. commun.) also showed that, for a post in the ground, the

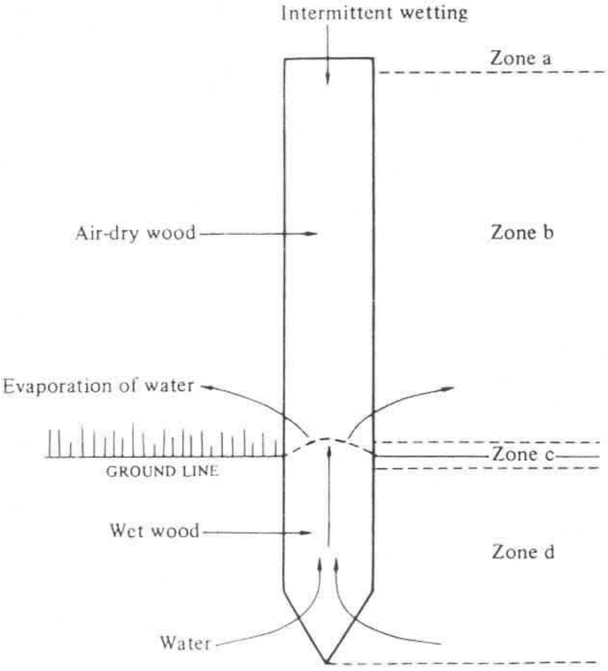


Fig. 4. Water movement in a fence post which produces ecological zones for the colonisation and development of micro-organisms.

equilibrium moisture contents of the four zones along its length will remain constant, but nevertheless water will move from zone (*d*) to zone (*c*) and will evaporate at the boundary between zones (*c*) and (*b*). In this region, materials dissolved in or carried by the water will be deposited where evaporation takes place. This is the ground-line region where the most active decay occurs and any such materials may be nutrients for the decay organisms present. Above the ground line, the movement of air across the surface dries the wood to moisture contents at which decay cannot take place. It is thus only at, or near, the ground line that the conditions are both wet enough and yet sufficiently aerobic to allow fungal growth. It is in this region of the post that biodeterioration will occur. The loss of strength which results is normally caused by decay by basidiomycetes, and is the climax of a series of events which have taken place since the post was first put into the ground. Yet basidiomycetes cannot be isolated for at least the first three months of exposure, (Corbett & Levy, 1963; Butcher, 1971; Käärik, 1967, 1968; Banerjee & Levy, 1971; Clubbe, 1978).

Cowling (1965), discussing the nutritional aspects of wood-inhabiting fungi including the basidiomycetes, pointed out the importance of the low nitrogen content of wood. He also considered the availability of cellulose in cell walls and how far the other wall constituents prevented breakdown of the cellulose. Cowling & Merrill (1966) also discussed nitrogen relationships of wood and its rôle in wood deterioration. Greaves (1966) demonstrated that readily available food reserves in the parenchyma of the rays of the sapwood are also important for the initial colonisation of the wood. In laboratory experiments with monocultures of fungi and bacteria, he showed that the ray parenchyma was usually the first tissue to be substantially colonised prior to the initiation of decay of the cell walls. If the nutrients are water soluble they can move through wood and be deposited near the surfaces of cut timber in normal drying and seasoning processes (King, Oxley & Long, 1974). Evaporation from the surface causes a movement of water and materials in solution towards the surfaces, and the solutes remain as food sources which encourage scavenging micro-organisms to colonise wood.

Although wood is initially a nitrogen-poor environment for basidiomycetes, the nitrogen content can increase by microbial and physical effects. Sharp & Millbank (1974), Levy *et al.* (1974), Baines & Millbank (1976) and Baines *et al.* (1977) demonstrated that the phenomenon of nitrogen fixation can occur in wood providing it is wet enough. Baines & Millbank (1976) also demonstrated the progressive penetration of nitrogen-fixing organisms into wood from an exposed face, probably via the ray parenchyma. Uju (1979) carried out an investigation of the nitrogen relationships of wood in ground contact, by adding a solution of a soluble inorganic nitrate to sterile soil in which sterile sticks of Scots pine had been half buried. He showed that an increase in nitrogen content took place not only in that half of the stick below soil level but also in the half projecting above the soil level. He subsequently demonstrated this increase in nitrogen in the wood above ground level in a variety of conditions, and produced evidence to show that some of the increase was due to the movement of soluble nitrogen, since it could not be correlated with the presence of any organism (Uju, Baines & Levy, 1980).

Succession and climax of micro-organisms in sapwood stakes

Clubbe (1978, 1980) analysed a field experiment of Scots pine and birch sapwood stakes some of which had been treated with a wood preservative. He emphasised that the identification of individual species did not help to determine patterns of succession amongst the colonising organisms or provide a clue to their importance in the onset and development of decay. However, if the effect of each individual organism on the wood structure was taken into account, it was possible to group them into the categories described earlier in this Chapter and listed in Table 1. It was then possible to see patterns of development in both colonisation and decay.

The results of Clubbe's isolation technique showed the colonisation of birch sapwood stakes at the ground line in the course of a year by the six groups of organism. The bacteria appeared first and were the first colonisers at each depth, but they were isolated with decreasing frequency towards the end of the year. They were followed by the 'primary moulds' which also decreased towards the end of the year. The 'stainers' followed the 'primary moulds' and also showed some decline by the end of a year. The 'soft rots' and basidiomycetes did not appear until three months had elapsed. Both groups had penetrated to 40 mm depth at six months, after which the 'soft rots' declined in frequency of isolation whilst the basidiomycetes were clearly the dominant mycoflora with a very high percentage frequency. The 'secondary moulds' followed the basidiomycetes and built up in importance with them. Thus there appeared to be a clearly defined succession of the mycoflora, with the basidiomycetes forming the climax.

A similar sequence of events was shown to occur in Scots pine stakes, although it took a longer time, with no colonisation to 40 mm depth from the exposed tangential surface for the first nine months. There was some decline in the frequency of isolation of bacteria and 'primary moulds' by the end of a year, whilst the basidiomycetes were clearly increasing and appeared likely to become the climax organisms. The soft-rot fungi were never a major component of the mycoflora, whilst the 'secondary moulds' were building up at the end of the year.

A direct observation technique (Clubbe, 1980) confirmed these observations and showed some soft-rot decay in birch and a very small amount in Scots pine. After eighteen months exposure, considerable basidiomycete decay had occurred in both species at a depth of 3 mm from the exposed tangential surface, with birch showing greater decay. Dickinson (Chapter 10) quotes Clubbe's results from the preservative-treated stakes, where the presence of the preservative eliminated basidiomycetes from the mycoflora, and in their absence the 'soft rots' took over as a climax group of organisms. In treated birch there was clear evidence of soft-rot attack, whilst in Scots pine there was no sign of wall decay although these organisms were isolated with high percentage frequency.

The rôle of basidiomycetes

It is quite clear from the subjective qualitative observations of many researchers, and from the objective quantitative studies of Clubbe, that in normal wood in ground contact the wood-rotting basidiomycetes form the climax of the succession of colonising micro-organisms and are the main cause of decay. However, they first appear late in the succession and it is clear from Clubbe's work (Dickinson: Chapter 10) that even a mild loading of wood preservative eliminates them altogether and allows the soft-rot fungi to become the climax mycoflora. Further work is needed to determine the reasons for both these phenomena, but a number of factors may be concerned:

(*a*) the stake is dry when first put into the ground and may take some time to absorb enough water from the soil to support basidiomycete growth;

(*b*) once the wood gets wet it becomes too wet for the basidiomycetes, and time is required for bacteria to destroy the pit membranes which permits gaseous diffusion and gives rise to less anaerobic conditions;

(*c*) insufficient nitrogen and nutrients may be present until enough time has elapsed for the wick action, by which water moves along the grain, to have built up the nutrient content to a level necessary for the basidiomycetes;

(*d*) spore germination studies (Carey, 1980; J. K. Carey & J. G. Savory, unpublished) have shown that spores of *Gloeophyllum trabeum* will germinate on freshly-felled, green, wood but not on wood that has subsequently been kiln-dried, unless it has been colonised by bacteria and fungi;

(*e*) the fact that soft-rot fungi rapidly form the climax mycoflora when basidiomycetes are unable to colonise suggests a possible interaction between these two groups. Time may be required to enable the basidiomycetes to become dominant.

Conclusions

The wood-rotting basidiomycetes will normally become the climax mycoflora in wood in contact with the ground, and will be the major cause of decay. They do not, however, colonise the wood for at least three months, during which time a succession of organisms occur, some of which can cause partial breakdown of the wood, but normally the only other group of wood-rotting organisms, the soft-rot fungi, play a minor rôle, and are dominated and possibly suppressed by the basidiomycetes. If for any reason the basidiomycetes are eliminated from the mycoflora, the 'soft rots' take on a much more active rôle and become the climax group present.

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